

## New Simrothiellidae (Mollusca: Solenogastres) from the Mozambique Channel, Western Indian Ocean

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**Abstract.** Five new species of Solenogastres sampled in the Mozambique Channel near the Comoro Islands, northwest Indian Ocean, are described herein. The specimens were collected in water depths between 520 m and 3716 m from soft sediments ranging from clay to muddy sand. They belong to the family Simrothiellidae Salvini-Plawen, 1978, based on radula morphology, histology of the ventral foregut glands, and the presence of copulatory stylets and respiratory folds. One species is placed in the genus *Simrothiella* Pilsbry, 1898, two in *Kruppomenia* Nierstrasz, 1903, and two in *Spionomenia* Arnofsky, 2000. The names *Simrothiella comorensis*, *Kruppomenia macrodoryata*, *Kruppomenia nanodentata*, *Spionomenia praematura*, and *Spionomenia phaseolosa* are proposed. Species descriptions utilize features of internal anatomy and histology as well as hard part morphology.

### INTRODUCTION

The Simrothiellidae are a diverse family of the molluscan class Solenogastres (= Aplacophora, partim: subclass Neomeniomorpha sensu Scheltema) recently comprising 18 species within eight genera, the number of species increasing steadily. Although some interstitial representatives such as *Biserranenia psammobionta* Salvini-Plawen, 1968, inhabit subtidal sands, most simrothiellid species are found on clay or muddy sand in greater depths down to the abyssal zone (*Helicoradomenia juani* Scheltema & Kuzirian, 1991), even at hydrothermal vents (*Helicoradomenia bisquama* and *Helicoradomenia acredema* Scheltema, 2000).

The family is well defined by a radula composed of biserial radula bars with numerous denticles and by paired ventral salivary glands with epithelial gland cells (type C after Salvini-Plawen, 1978). Integumental sclerites are generally hollow needles with simple or differentiated (hooked, captate) tips, with the exception of the genus *Helicoradomenia* defined exclusively by solid spicules. Copulatory stylets are present in most genera.

### MATERIALS AND METHODS

The specimens were sampled in the northern region of the Mozambique Channel (Comoro Islands), northwest Indian Ocean, in the course of the Campagne Benthedi (17.3.–14.4.1977) of the Centre National de Tri d'Océanographie Biologique (CENTOB, Brest). They were collected in depths ranging from 520 m to 1716 m on fine sediments (Table 1) and preserved in 70% ethanol.

Type specimens were photographed using a dissecting microscope. Measurements of the small animals were made by means of an ocular micrometer. Length is defined as the axial midline in lateral view, height as the

medial diameter in lateral view. Mantle spicules were removed in a drop of 70% ethanol on a microscopic slide using needles or fine bristles, then air dried and permanently mounted in epoxy resin (Araldit). Spicule types were identified, measured, and drawn using a light microscope equipped with an ocular micrometer. The decalcified specimens were serially sectioned (2 µm) in epoxy resin (Araldit) and stained with Methylene Blue—Azure II (Richardson et al., 1960). Reconstructions of fore and/or hind ends are presented in a lateral perspective, reconstructions of radula bars in a frontal view.

Type specimens (slides of spicule preparations and serial sections, undissected paratypes only for *Spionomenia praematura*) are deposited in the Muséum National d'Histoire Naturelle de Paris, France.

The terminology in this paper follows Salvini-Plawen, 1985, with some changes and additions: *Radial* mantle spicules protrude vertically from the mantle surface. *Oblique* spicules protrude in angles of about 35°–70° from the mantle surface and point posteriorly. *Skeletal* spicules (tangential spicules, Hoffman, 1949) are likewise obliquely arranged but protrude in very low angles below 20° from the mantle epithelium and consequently are embedded within the cuticle in several layers. They are oriented in angles of about 45° to each side of the longitudinal body axis, thus forming a network of intercrossing elements. *Captate* spicules are characterized by pointed, asymmetrically broadened apical ends; the *radular buttress* is a lateral thickening or reinforcement of a radula bar (Arnofsky, 2000; Scheltema & Schander, 2000). *Epidermal papillae* are stalked glandular cell-groups opening onto the cuticle surface, whereas *epidermal gland cells* are oval and do not protrude through

Table 1

BENTHEDI (CENTOB) localities in the Moçambique Channel where Simrothiellidae were sampled in 1977. The sampling sites are type localities for the described species. S. com., *Simrothiella comorensis*, sp. nov.; K. ma., *Kruppomenia macrodoryata*, sp. nov.; K. na., *Kruppomenia nanodentata*, sp. nov.; S. pr., *Spiomenia praematura*, sp. nov.; Sp. ph., *Spiomenia phaseolosa*, sp. nov.

Sample BEN- THEDI	Depth (m)	Latitude (south)	Longitude (east)	Sediment	Number of specimens per species				
					S. com.	K. ma.	K. na.	Sp. pr.	Sp. ph.
37 DR	830–520	12°53'	45°16'	sandy clay			1		
40 DR	1480	12°56'	45°18'	yellow, muddy sand with sponge spic- ules				5	
87 CH	3716	11°44'	47°35'	clay and debris	1	1			2

the cuticle. The term *vestibulum* is preferred to the term atrial sense organ.

## SYSTEMATICS

Simrothiellidae Salvini-Plawen, 1978

Type genus *Simrothiella* Pilsbry, 1898

**Diagnosis:** Mantle spicules solid or hollow; common vestibulo-buccal opening; radula with biserial bars; ventral salivary glands as ampullae with epithelial gland cells (type C) (Figure 1).

The family comprises eight genera: *Simrothiella* Pilsbry, 1898; *Cyclomenia* Nierstrasz, 1902; *Kruppomenia* Nierstrasz, 1903; *Biserramenia* Salvini-Plawen, 1968; *Birasoherpia* Salvini-Plawen, 1978; *Helicoradomenia* Scheltema & Kuzirian, 1991; *Plawenia* Scheltema & Schander, 2000; *Spiomenia* Arnofsky, 2000. *Sialoherpia* Salvini-Plawen, 1978, was tentatively classified within Simrothiellidae but subsequently removed and placed into Pararrhopaliidae (Garcia-Alvarez et al., 2001).

*Simrothiella* Pilsbry, 1898

**Synonyms:** *Solenopus* Sars, partim.

**Type species:** *Solenopus margaritaceus* Koren & Danilssen, 1877 (ICZN, 1981).

**Diagnosis:** Cuticle thick; mantle spicules hollow, acicular; skeletal, radial, and oblique spicules present, with paired anteroventral radular pockets, radula bars with elongated lateral denticle; dorsoterminal sense organ present; secondary genital opening single; copulatory stylets present; pallial cavity with respiratory folds.

Besides the new species recorded here, so far only the type species has been described within the genus.

*Simrothiella comorensis* Todt & Salvini-Plawen,  
sp. nov.

**Holotype:** BENTHEDI (CENTOB) 87CH, 11°44'S, 47°35'E, 3716 m; mantle spicules (1 slide), series of histologic cross-sections (18 slides).

**Diagnosis:** Oblong species; acicular mantle spicules short and slender; mantle without epidermal papillae; mantle cavity with a pair of long, anteroventral pouches confluent with paired copulatory stylet sheaths; vestibulum with clusters of numerous slender papillae; radular pockets ventrolaterally spiraled, radula bars with 10 small denticles and a single, much longer, curved lateral denticle; single pair of copulatory stylets measuring almost 1/3 total body length.

**Description (Figures 2A, 3A, 4A–C):** Body of the single specimen cylindrical, 1.9 mm in length, 0.6 mm in height, pedal groove exposed. Vestibular opening oval; mantle evenly covered by slightly curved to sinuous, hollow, oblique spicules, giving animal a rough appearance. Skeletal and radial spicules present, but most spicules oblique. Cuticle thickness 60 µm ventrally, 30 µm dorsally. Spicules thick-walled, 60 µm to 80 µm in length ventrally, up to 130 µm laterally and dorsally. Largest spicules sinuous to S-shaped, smaller spicules curved or recurved (Figure 4A). Distal part of spicules solid, compressed, 10 to 15% total spicule length.

Vestibulum provided dorsofrontally with numerous slender papillae grouped in dense tufts of six to 10 papillae. Pedal gland large. Pedal fold single, narrow, ending in front of pallial cavity opening. Sole glands small, decreasing in number posteriorly. Pallial cavity divided into a dorsal portion terminally bearing respiratory folds and a pair of tubelike anteroventral pouches (Figure 4C), 60 µm long, surrounded by a thick muscular layer, and holding distal part of one copulatory stylet (Figure 3A).

Pharynx muscular, lined by epithelial gland cells which are most numerous dorsally. No anterodorsal midgut caecum. Radula (Figures 2A, 4B) 200 µm long with 20 rows of paired bars. Lateroventral radular pockets short, spiraled, with 10 bars each. Bars strong and curved, 90 µm in greatest dimension, 25 µm in height, 25 µm in width medially; laterally thickened and bearing a curved denticle 40 µm long, circular in cross-section, and positioned at right angle to the bar. Dorsal margin of bar with 10

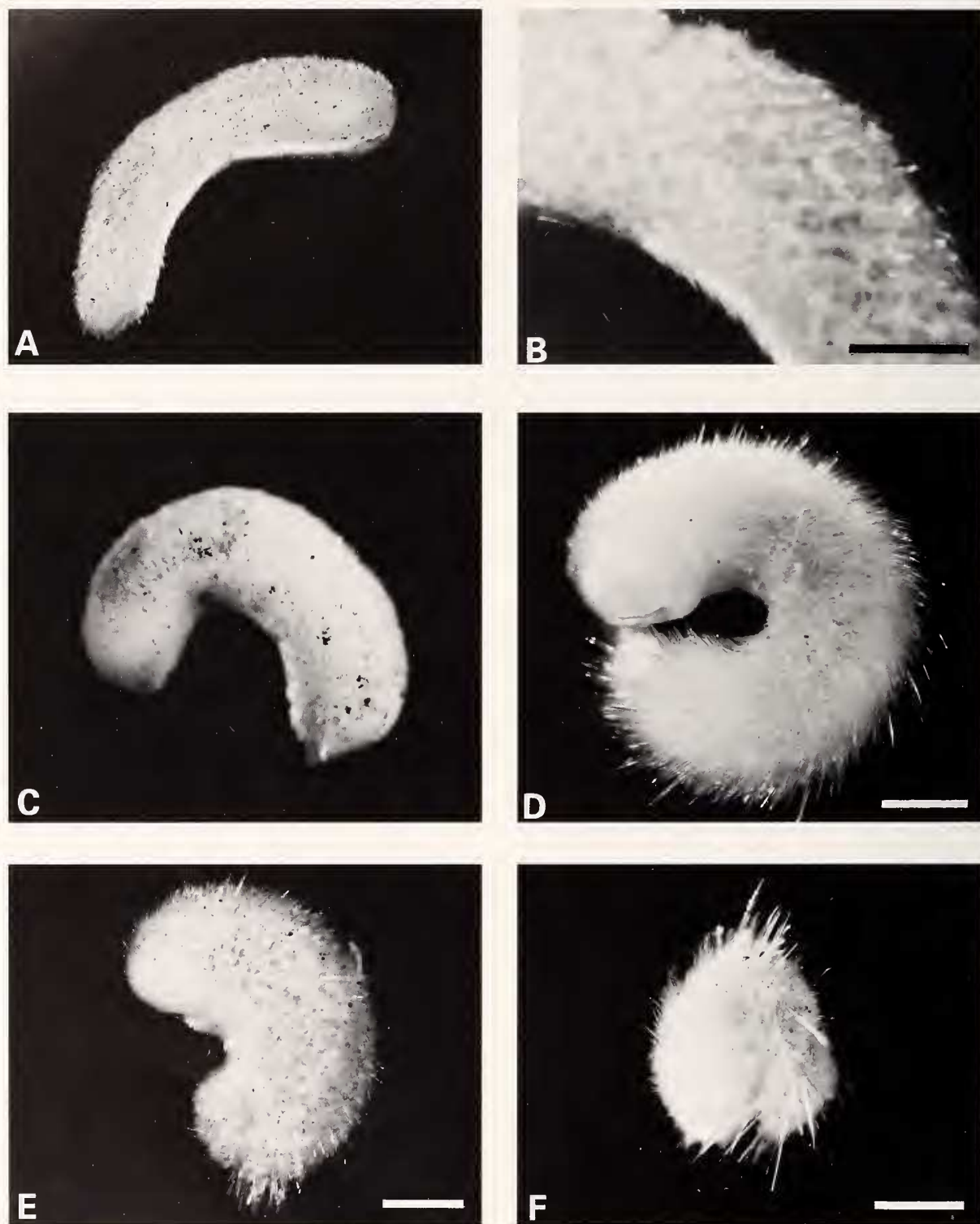


Figure 1. Simrothiellidae of the BENTHEDI cruise, animals in lateral view. A, B. *Kruppomenia macrodoryata* Todt & Salvini-Plawen, sp. nov., holotype: A. Entire animal, anterior end to the right, scale bar 0.5 mm. B. Detail showing the characteristic honeycomblike mantle surface, scale bar 0.25 mm. C. *Kruppomenia nanodentata* Todt & Salvini-Plawen, sp. nov., holotype, anterior end to the left, scale bar 0.4 mm. D. *Spiomenia praematura* Todt & Salvini-Plawen, sp. nov., paratype 4, showing the slitlike vestibular opening and the furry appearance of the mantle spicules, scale bar 0.5 mm. E, F. *Spiomenia phaseolosa* Todt & Salvini-Plawen, sp. nov. E. Holotype, immature specimen, anterior end to the left, scale bar 0.4 mm. F. Paratype 1, juvenile specimen, scale bar 0.1 mm.



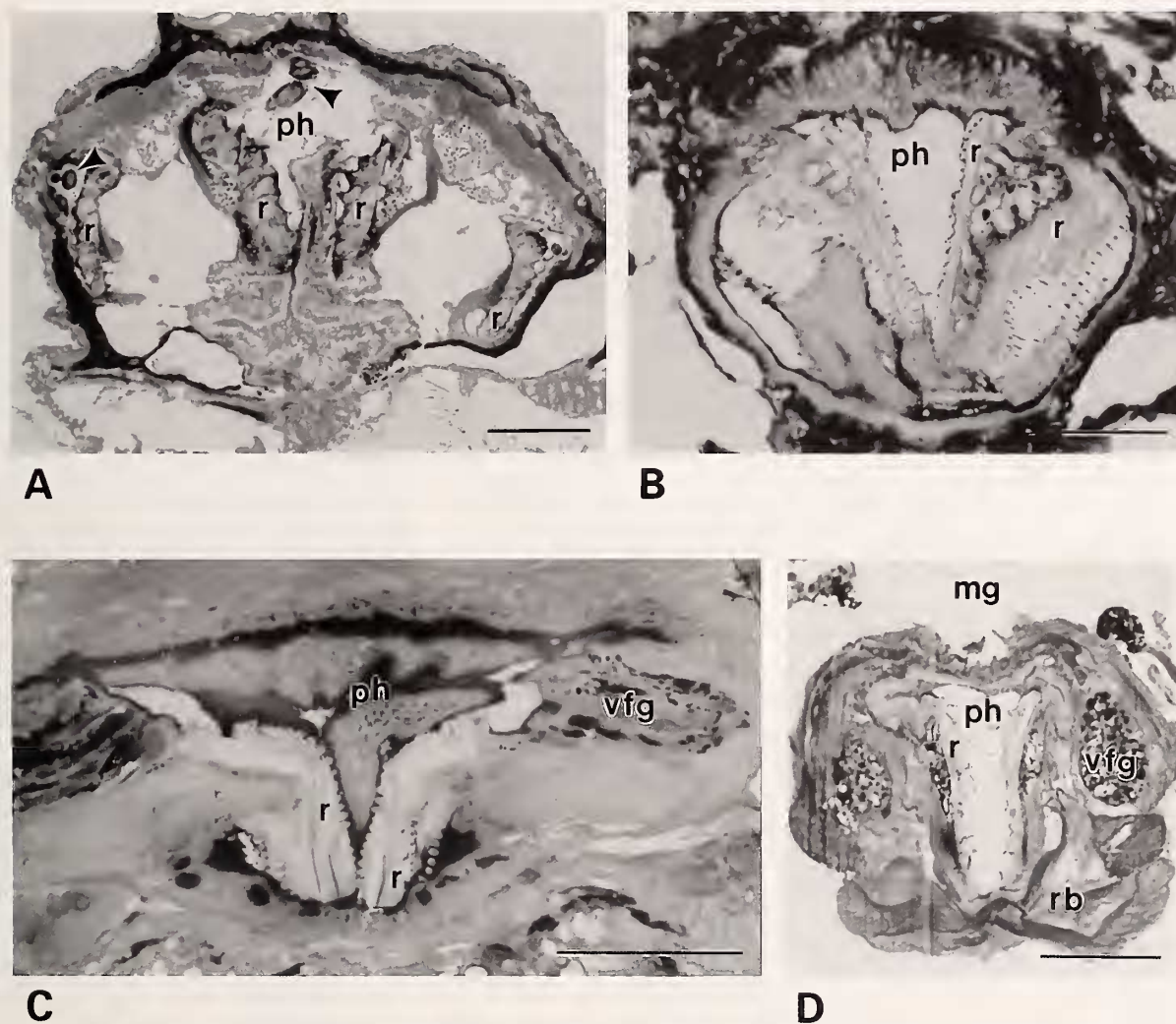


Figure 2. A. *Simrothiella comorensis* Todt & Salvini-Plawen, sp. nov., holotype, histologic section of the anterior portion of the radular apparatus showing a pair of radula bars medially and the paired radular pouches containing further radula bars laterally; the elongated lateral denticles are represented in cross-section (arrowheads), scale bar 50  $\mu$ m. B. *Kruppomenia macrodoryata* Todt & Salvini-Plawen, sp. nov., holotype, histologic section showing the radular apparatus in the region of the bend into paired, lateral radular pockets, scale bar 25  $\mu$ m. C. *Spiomenia praematura* Todt & Salvini-Plawen, sp. nov., paratype 1, histologic section showing the radular apparatus with the ventral foregut glands lateral, scale bar 50  $\mu$ m. D. *Spiomenia phaseolosa* Todt & Salvini-Plawen, sp. nov., histologic section showing a pair of radula bars and the ventral foregut glands, scale bar 50  $\mu$ m. Key: mg, midgut; ph, pharynx; r, radula bar; rb, radular bolster; vfg, ventral foregut gland.

denticles: six pointed denticles, 6–8  $\mu$ m long, followed laterally by one curved denticle, 20  $\mu$ m long, at the thickened portion of the bar and three minute, curved denticles, 5–6  $\mu$ m long.

Unpaired and paired portions of the spawning duct approximately equal length, composed of large gland cells filled with mucus and deeply staining vesicles. Paired copulatory stylet sheaths about 500  $\mu$ m long, reaching almost midregion of body and posteriorly continuous with tubelike pouches of the pallial cavity (Figure 4C). Paired copulatory stylets about 600  $\mu$ m long, diameter in the midregion 30

$\mu$ m, curved, almost cylindrical and pointed at both ends; posterior ends protruding into pallial cavity.

**Remarks:** The paired gonad contained large oocytes but no spermatocytes. Most likely due to the bent position of the studied specimen's posterior body, the posterior ends of the copulatory stylets were positioned within posterolateral pouches of the pallial cavity (Figure 4C, last diagram).

The presence of hollow skeletal mantle spicules and the long lateral denticle of the radula bar leads us to clas-



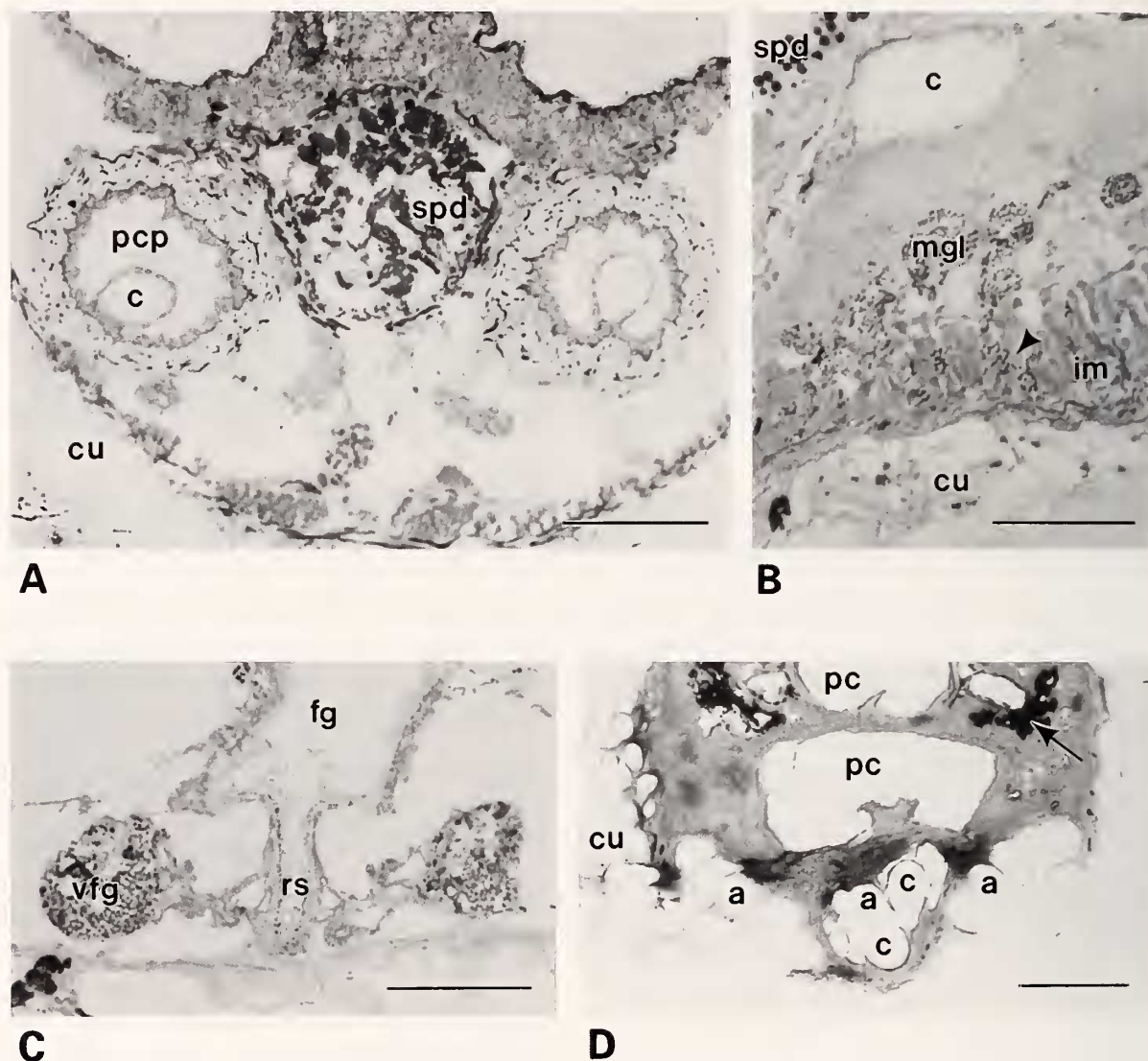


Figure 3. A. *Simrothiella comorensis* Todt & Salvini-Plawen, sp. nov., holotype, histologic section of the posterior body region with the unpaired spawning duct and the pair of tubelike pallial cavity pouches containing copulatory stylets, scale bar 50  $\mu$ m. B, C. *Kruppomenia nanodentata* Todt & Salvini-Plawen, sp. nov., holotype. B. Histologic section of the subepithelial gland cells of the mantle epithelium anterior to the pallial cavity opening, their proximal portions crossing the integumental muscle layer (arrowhead), scale bar 15  $\mu$ m. C. Histologic section showing the radular apparatus and the paired ventral foregut glands, scale bar 50  $\mu$ m. D. *Spiomenia praematura* Todt & Salvini-Plawen, sp. nov., holotype, histologic cross-section of the posterior body in the region of pallial cavity with suprapallial glands (arrow), showing the arrangement of pallial spines, scale bar 50  $\mu$ m. a: hole in the cuticle left by pallial spine; c: holes left by copulatory stylets; Key: cu, cuticle; fg, foregut; im, integumental muscles; mgl, mantle glands; pc, pallial cavity; pcp, pouch of pallial cavity; rs, radular sheath; spd, spawning duct; vfg, ventral foregut gland.

sify the present specimen as a species of the now monotypic genus *Simrothiella*. In contrast to *S. margaritacea*, *S. comorensis* is characterized by radula bars with larger denticles at the dorsal margin and three small, curved denticles lateral to the elongated denticle, which is relatively smaller than in *S. margaritacea*, and by short, lateroventral, not long, ventral radula pockets. The prominent epidermal papillae described for *S. margaritacea*

(Odhner, 1921) do not occur in *S. comorensis*. The copulatory stylets of *S. comorensis* are much longer. Further details of the anatomy of the genital tract cannot be discussed owing to deficiencies in preservation of the more delicate epithelia.

**Etymology:** The species name *comorensis* refers to the Comoro islands as the type locality.

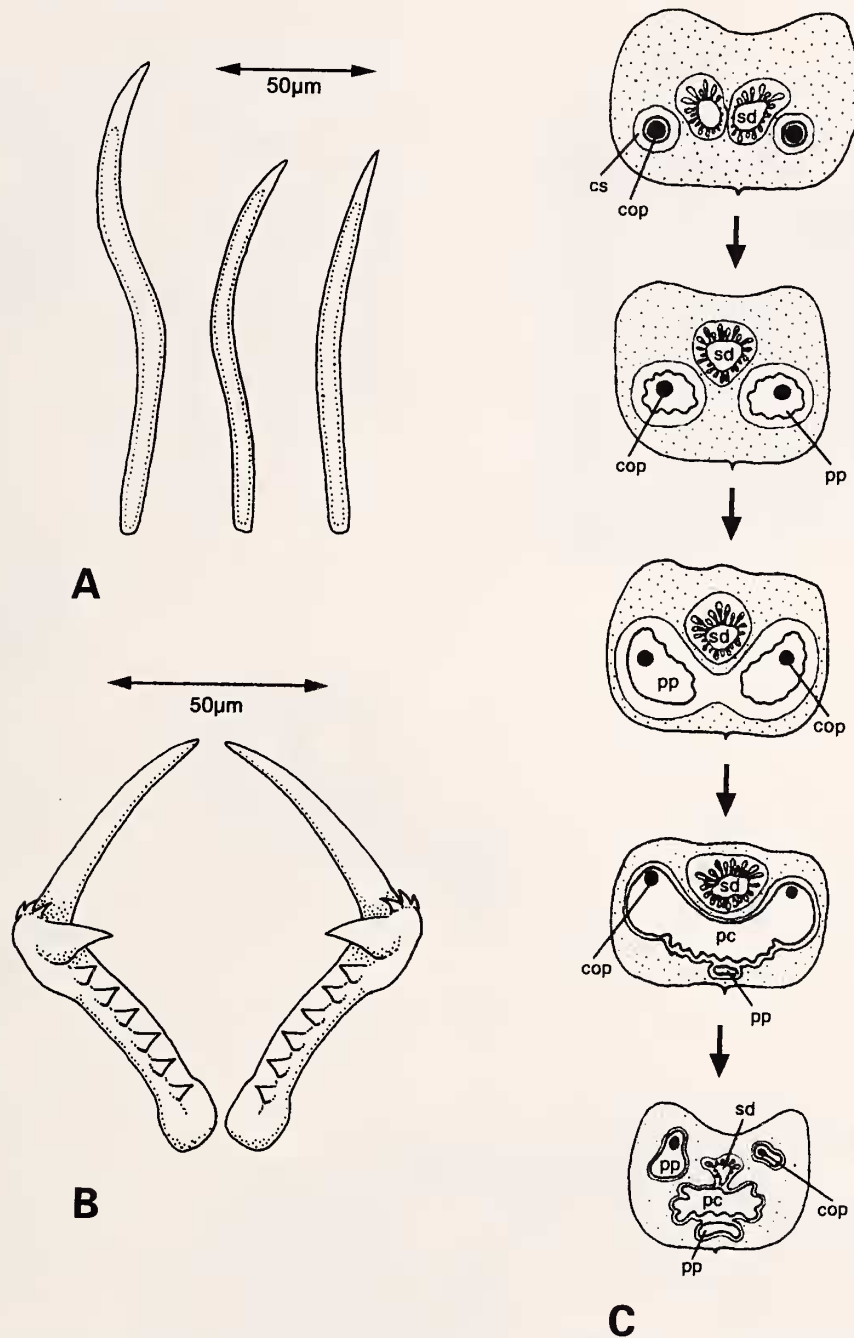


Figure 4. *Simrothiella comorensis* Todt & Salvini-Plawen, sp. nov. A–C. Holotype: A. Mantle spicules. B. Reconstructed pair of radula bars from the midregion of the radula. C. Schematic drawings of a series of cross-sections of the posterior body region. Key: cop, copulatory stylet; cs, copulatory stylet sheath; pc, pallial cavity; pp, pouch of pallial cavity; sd, spawning duct.

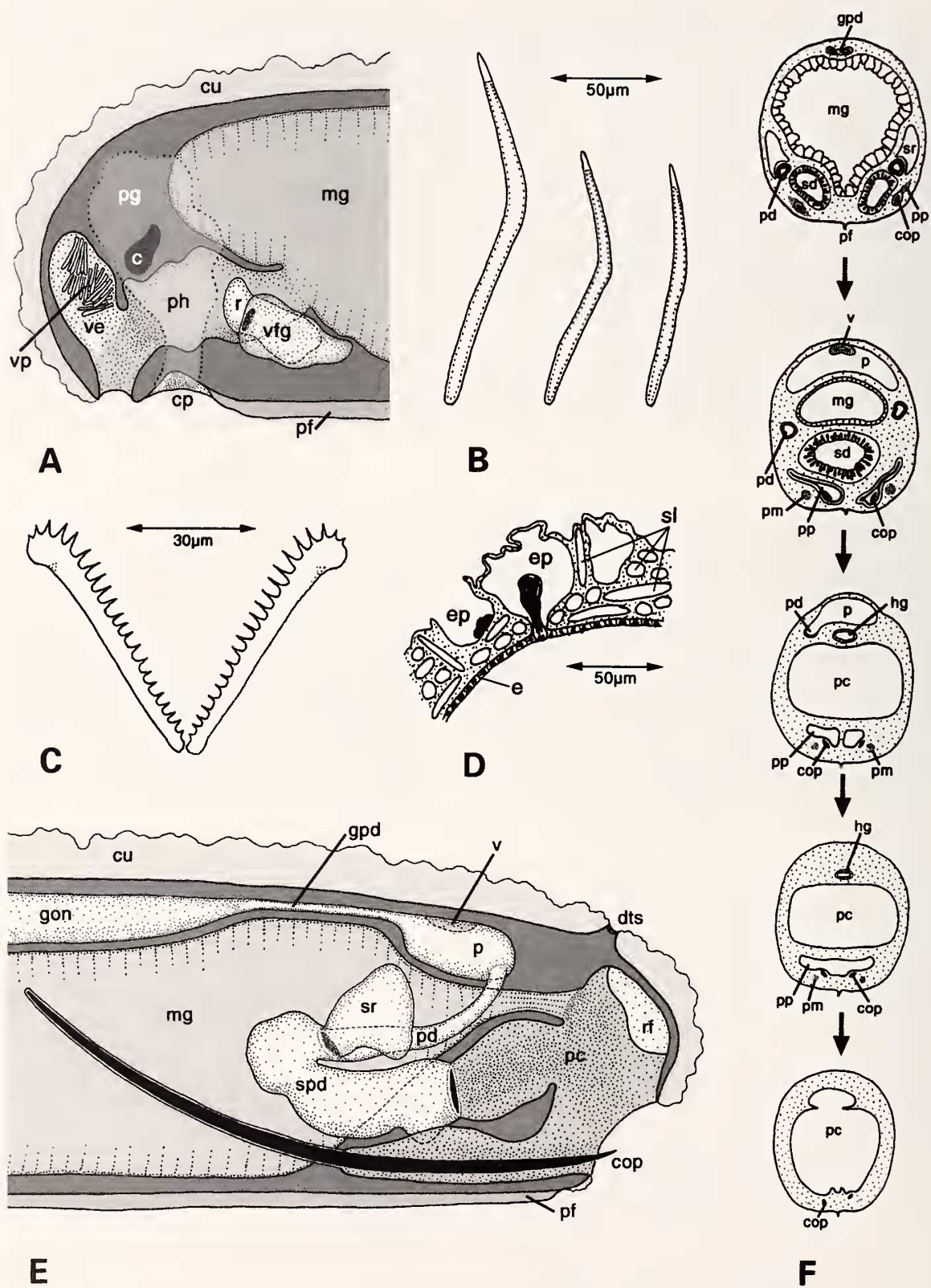
*Kruppomenia* Nierstrasz, 1903

**Type species:** *Kruppomenia minima* Nierstrasz, 1903.

**Synonyms:** *Simrothiella* Pilsbry partim in Salvini-Plawen 1972.

Salvini-Plawen (1972) classified *Kruppomenia minima*

Nierstrasz, 1903, and *K. borealis* Odhner, 1921, within the genus *Simrothiella* Pilsbry. Later he described the new species *Simrothiella schizoradulata* Salvini-Plawen, 1978, and *S. (?) rhynchota* Salvini-Plawen, 1978. Based on a study of new material, Scheltema & Schander (2000) reconstituted the genus *Kruppomenia* and placed *S. schizoradulata* in a





new genus *Plawenia*. In this paper we follow their conclusions. Consequently, *S. rhynchota* is here placed in *Kruppomenia* on the basis of the comblike structure of radula bars without an elongated lateral denticle.

**Diagnosis:** Cuticle thick; mantle spicules hollow, acicular or barbed; skeletal, radial, and oblique spicules present; with paired anteroventral radular pockets; radula bars narrow, with numerous small denticles; seminal vesicles and/or paired seminal receptacles present; secondary genital opening single; copulatory stylets present; pallial cavity with respiratory folds; dorsoterminal sense organ present.

There are five described species: *K. minima* Nierstrasz, 1903; *K. borealis* Odhner, 1921; *K. rhynchota* (Salvini-Plawen, 1978); *K. levis* Scheltema & Schander, 2000; *K. delta* Scheltema & Schander, 2000.

*Kruppomenia macrodoryata* Todt & Salvini-Plawen, sp. nov.

**Holotype:** BENTHEDI (CENTOB) 87CH, 11°44'S, 47°35'E, 3716 m; mantle spicules (2 slides), series of histologic cross-sections (17 slides).

**Diagnosis:** Body oblong, small; mantle with large epidermal papillae; mantle spicules acicular and thin-walled, skeletal spicules forming an open meshwork, radial and oblique spicules curved; pallial cavity with a pair of long, anteroventral pouches; vestibulum with slender papillae arranged in clusters; anteroventral radular pockets shortly spiraled; radula bars slender with about 22 almost uniform denticles; ventral foregut glands oblong; midgut with anterodorsal caecum; single pair of copulatory stylets almost half as long as the whole animal.

**Description (Figures 1A, B, 2B, 5A–F):** Body cylindrical, 2.5 mm in length, 0.5 mm in height; anterior end rounded, posterior end slightly tapered (Figure 1A). Mantle surface with honeycomblake appearance due to regularly scattered protusions of the cuticle combined with relatively short spicules (Figure 1B). Pedal groove with row of fragile scales and a band of thickset hollow spicules on each side. Cuticle thickness 40–90  $\mu\text{m}$  including large, flasklike epidermal papillae protruding into it (Figure 5D). Seven to 10 papillae per cross-section (2  $\mu\text{m}$ ) are common. Spicules thin-walled, 40–200  $\mu\text{m}$  long and

5–12  $\mu\text{m}$  wide (Figure 5B). Most common are radial spicules, skeletal spicules forming an open meshwork. Spicules with short solid tips and bent above midpoint, proximal end slightly recurved. Spicules lining vestibular and pallial cavities and near pedal groove of same shape but smaller (40–80  $\mu\text{m}$ ) than spicules of dorsal mantle area.

Vestibular papillae slender, about 50  $\mu\text{m}$  long, arranged in paired lateral rows and one posterior median bundle (Figure 5A), containing small secretory vesicles. Dorsoterminal sense organ single, situated above the pallial cavity. Pedal fold single throughout, running from pedal pit to pallial cavity. Pedal gland large, sole glands along the pedal groove few, small.

Pallial cavity with three areas (Figure 5E): posterodorsal portion with about 11 respiratory folds; midportion frontally with anus and secondary genital pore; ventral portion frontally with two tubelike pouches covered by circular muscle tissue, with copulatory stylets (Figure 5F). Opening of pallial cavity with a row of about five abdominal spicules on each side. Integumental muscle layers thin, ventral longitudinal muscles pronounced. Dorsoventral muscle fibers few, restricted to anterior body region.

Mouth opening at posterior end of vestibulum. Pharynx with thin longitudinal and thick circular muscle layer interlaced by single radial fibers; epithelial secretory cells anteriorly numerous, containing heavily staining vesicles. Radula (Figure 2B) biserial, 70  $\mu\text{m}$  wide, 230  $\mu\text{m}$  long, with about 35 paired bars; anteroventral radular pockets paired, each with about 13 radula bars. Bars slender, almost straight, lateralmost portion slightly bent (Figure 5C), 60  $\mu\text{m}$  broad, 4  $\mu\text{m}$  in height, 5  $\mu\text{m}$  thick. The 18–22 denticles shortest medially (2  $\mu\text{m}$ ), up to 5  $\mu\text{m}$  laterally, with sharply pointed curved tips. Ventral foregut glands as oblong ampullae adjacent to radula, composed of epithelial glandular cells, covered by thin muscular layer. Midgut with anterodorsal caecum; hindgut short, opening into dorsal portion of pallial cavity.

Gonopericardioducts paired anteriorly, fusing to a single duct at midportion. Pericardium with ventricle attached to dorsal wall; pericardioducts opening at posterior end of pericardium and curving anteriorly to merge with posteriorly running spawning ducts. Seminal receptacles single, large, opening into pericardioducts shortly before

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Figure 5. *Kruppomenia macrodoryata* Todt & Salvini-Plawen, sp. nov. A–F. Holotype. A. Schematic diagram of the anterior body. B. Mantle spicules. C. Reconstructed pair of radula bars from the midregion of the radula. D. Schematic diagram of a cross-section of epidermis and decalcified cuticle showing large epidermal papillae and the orientation of spicules. E. Schematic diagram of the posterior body. F. Series of cross-sections from the midgut region posteriorly to the pallial cavity. Key: c, cerebral ganglion; cop, copulatory stylet; cp, ciliary pedal pit, indicated by dotted line; cu, cuticle; dts, dorsoterminal sense organ; e, epidermis; ep, epidermal papilla; gon, gonad; gpd, gono-pericardial duct; hg, hindgut; mg, midgut; p, pericardium; pc, pallial cavity; pd, pericardial duct; pf, pedal fold; pg, pedal gland; ph, pharynx; pm, protractor muscle of copulatory stylet; pp, pouch of pallial cavity; r, radula; rf, respiratory fold; sd, spd, spawning duct; sr, seminal receptacle; v, heart ventricle; ve, vestibulum; vfg, ventral foregut gland; vp, vestibular papillae.

their junction with spawning ducts. Spawning ducts fused about  $\frac{1}{3}$  of their way to pallial cavity, covered by circular muscles. Single pair of curved copulatory stylets, 1 mm long, almost half the total length of animal; anterior portion within sheath almost cylindrical, midregion laterally compressed, measuring  $35\ \mu\text{m} \times 10\ \mu\text{m}$  in cross-section, posterior portion tapering. Stylet sheath with layer of longitudinal muscles posteriorly confluent to single muscle bundle fixed to body wall posterolateral to pallial cavity.

**Remarks:** In the present specimen the long, tubelike ventral pallial pouches for the copulatory stylets are compressed and thus no lumina are visible.

The placement of the species in the genus *Kruppomenia* is based on the presence of hollow skeletal mantle spicules, copulatory stylets, and slender radular bars with numerous small denticles. The denticulation of the radula bars, however, with a relatively low number of denticles compared to other representatives of the genus, and the long copulatory stylets represent distinct features to define the species.

**Etymology:** *Macrodoryata* from Greek *makros* (large) and *dory* (rod) referring to long copulatory stylets.

*Kruppomenia nanodentata* Todt & Salvini-Plawen, sp. nov.

**Holotype:** BENTHEDI (CENTOB) 37DR,  $12^{\circ}53'S$ ,  $45^{\circ}16'E$ , 830–520 m; mantle spicules (1 slide), series of histologic cross-sections (10 slides).

**Diagnosis:** A small, stout species with relatively short, thin-walled acicular spicules; mantle without epidermal papillae but with epidermal gland cells forming a ventral glandular mass anterior to pallial cavity opening; vestibulum with branched, slender papillae in clusters; radula small, radular bars fragile with numerous tiny denticles and a small lateral hook; ventral foregut glands oval; midgut without anterodorsal caecum; single pair of copulatory stylets.

**Description (Figures 1C, 2B, C, 6A–D):** Body light brown, cylindrical, 3.5 mm in length and 0.6 mm in height, posterior end slightly broadened (Figure 1C). Mantle surface covered by short spicules resulting in almost smooth outline, longer spicules at ventral groove and margin of pallial cavity opening. Vestibular opening and pedal groove clearly visible, pallial cavity opening covered by spicules.

Cuticle thickness  $45\ \mu\text{m}$  ventrally,  $60\ \mu\text{m}$  dorsally. Skeletal and obliquely upright spicules most abundant, radial spicules rare. Spicules of two principal types (Figure 6C): type 1 between  $100\ \mu\text{m}$  and  $200\ \mu\text{m}$  long, slightly curved to recurved or double-bent with solid tips of up to 15% of total extension; type 2 more slender, length ranging between  $70\ \mu\text{m}$  and  $150\ \mu\text{m}$ , recurved, S-shaped or multiple-bent with long, curved tips making up 20–30% of total length.

Vestibulum with slender, branched papillae in clusters (Figure 6A). Pedal fold single to the opening of pallial cavity,  $20\ \mu\text{m}$  wide,  $25\ \mu\text{m}$  high; density of sole glands decreasing posteriorly. Pallial cavity with five long respiratory folds dorsally, and with paired anteroventral pouches,  $500\ \mu\text{m}$  long, continuous with the copulatory stylet sheaths.

Glandular cells of epidermis with transparent secretions and tiny dark vesicles; more numerous ventrally. Glandular mass of subepithelial gland cells, anteriorly bilobed, above and laterally to posterior end of pedal fold (Figure 3B), discharging through cuticle laterally to pedal groove via small interstices or fine ducts; secretional products very similar to epidermal gland cells. Integumental muscle layers thin, longitudinal muscle tissue pronounced ventrally. Dorsoventral muscle bundles forming strong retractors for pedal pit and foregut.

Pharynx with strong circular and longitudinal muscle layers, with evenly spread epithelial gland cells holding translucent, granular contents. Radula minute,  $70\ \mu\text{m}$  in total length, and consisting of 45 pairs of small bars, up to  $14\ \mu\text{m}$  in greatest dimension and  $2\ \mu\text{m}$  in height (Figure 6D). Distal margins of bars with numerous, tiny denticles and one larger curved denticle laterally. Radular pockets paired, with about 20 radular bars, spiraling lateroventrally in a single turn. Ventral foregut glands egg-shaped,  $160\ \mu\text{m}$  long,  $80\ \mu\text{m}$  wide, located on each side of radular sheath and attached to it by thin cords of connective tissue (Figures 3C, 6B), opening to pharynx lateroventral to radula. Midgut with small anterodorsal lobe, no proper caecum developed.

Paired pericardioducts from posterior end of pericardium ventrally, then anteriorly adjacent to roof of paired spawning ducts. Paired, anterior part of spawning duct slightly longer than unpaired part, with spongy epithelium, containing small, deeply staining, rodlike bodies; near junction of paired spawning ducts, epithelial cells with deeply staining secretions; epithelial cells of unpaired spawning duct with transparent secretion and dark globular vesicles larger than those of epidermal gland cells. Single pair of copulatory stylets,  $290\ \mu\text{m}$  long,  $14\ \mu\text{m}$  in maximum diameter, oval in cross-section, tapering slightly proximally and more obviously at the distal end. Stylet sheaths with circular muscle layer, posteriorly opening to paired anteroventral pouches of pallial cavity, protractor muscles from anterior end of sheath to lateroventral body wall.

**Remarks:** The paired gonad is small, indicating a possibly premature state of the animal, but holds oocytes and spermatocytes. The epithelium of the paired, anterior part of the spawning duct is spongy, containing small, deeply staining, rodlike bodies. This can be interpreted either as highly vascularized epithelium with cells containing glandular vesicles of a peculiar shape or as differentiation into numerous, small seminal vesicles holding sperm.

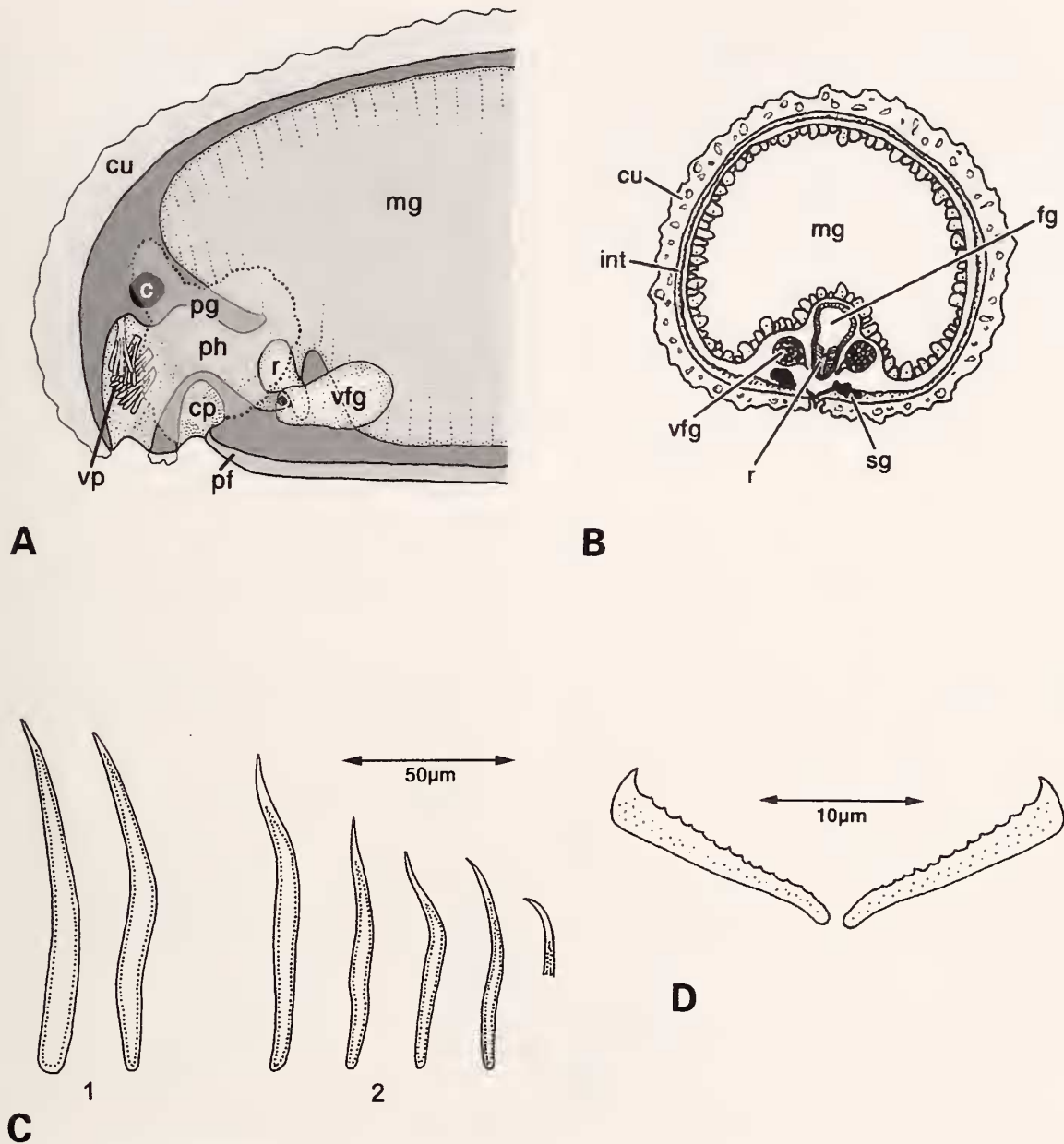


Figure 6. *Kruppomenia nanodentata* Todt & Salvini-Plawen, sp. nov. A–D. Holotype. A. Schematic diagram of the anterior body. B. Schematic diagram of a cross-section in the anterior body region showing the position of radular apparatus and ventral foregut glands. C. Mantle spicules of types 1 and 2. D. Reconstructed pair of radula bars from the midregion of the radula. Key: c, cerebral ganglion; cp, ciliary pedal pit; cu, cuticle; fg, foregut; int, integument; mg, midgut; pf, pedal fold; pg, pedal gland, indicated by dotted line; ph, pharynx; r, radula; sg, sole gland; vfg, ventral foregut gland; vp, vestibular papillae.

The presence of hollow, skeletal mantle spicules, of slender radular bars with numerous small denticles, and of copulatory stylets indicates a relationship to species in the genus *Kruppomenia*. However, the gland cells of the mantle epithelium differ from the stalked epidermal papillae typical for other species of *Kruppomenia*. In particular, the glandular mass anteroventral to the pallial cavity opening has not been described for *Kruppomenia* spe-

cies. The formation of seminal vesicles and receptacula could not be determined owing to poor preservation of the fragile epithelia. The radular apparatus is much smaller than in other known species of the genus.

**Etymology:** The species name *nanodentata* from Latin *nanus* (dwarf) and Latin *dentatus* (tooth bearing) refers to the minute radula bars.



*Spiomenia* Arnofsky, 2000

**Type species:** *Spiomenia spiculata* Arnofsky, 2000.

**Diagnosis:** Cuticle thick; mantle spicules hollow, thin-walled, partly with asymmetrically broadened tips (captate), exclusively oblique, no skeletal spicules; with paired anteroventral radular pockets, radula bars with lateral buttress, denticles heterogeneous, formed also lateral to the buttress; dorsoterminal sense organ present; secondary genital opening single; copulatory stylets present; pallial cavity with respiratory folds.

*Spiomenia praematura* Todt & Salvini-Plawen, sp. nov.

**Holotype:** BENTHEDI (CENTOB) 40DR, 12°56'S, 45°18'E, 1 480 m; mantle spicules (1 slide), series of histologic cross-sections (26 slides).

**Numbered paratypes:** Paratype 1: type locality; mantle spicules (1 slide), series of histologic cross-sections (20 slides); paratype 2 type locality; mantle spicules (1 slide), series of histologic cross-sections (14 slides); paratypes 3, 4: type locality; whole animals in 70% ethanol.

**Diagnosis:** A spiculose species with elongate body; longest mantle spicules acicular, captate spicules more slender with length of cap 1/5 to 1/6 of total length, opening of pallial cavity laterally with a paired row of (6) pallial spines; mantle without epidermal papillae; vestibulum small with few, very short papillae; suprapallial glands present; radula bars curved with 17 denticles, one small denticle laterally to the barely pronounced radular buttress; ventral salivary glands within buccal muscle tissue, midgut with anterodorsal caecum; genital tract unknown (all available specimens subadult); single pair of long copulatory stylets.

**Description (Figures 1D, 2C, 3D, 7A–C):** Body almost cylindrical, anterior and posterior ends slightly tapered, subadult holotype 3.6 mm long, 0.9 mm high. Spicules thickest, longest at posterior body end, regularly and unidirectionally arranged (Figure 1D). Vestibular opening triangular, pedal groove and pallial opening covered by spicules.

Cuticle 80  $\mu$ m high, dorsally somewhat thickened. Mantle spicules in one layer, hollow, thin-walled, slightly recurved (Figure 7B), of three different types: type 1 acicular, 500 to 600  $\mu$ m long, up to 25  $\mu$ m wide; type 2 acicular, 70 to 200  $\mu$ m long, 5 to 10  $\mu$ m wide. Types 1 and 2 with pointed, compressed solid tips of varying lengths but no longer than 15% of whole spicule length. Type 3 distally asymmetrically broadened (captate), with solid tips occupying about 15–25% of total length. Types 2 and 3 representing a continuum from acicular spicules with short tips to captate spicules. Small scales around dorsoterminal sense organ.

Vestibulum small, with few short and plump papillae

(Figure 7A); laterally covered by a thin layer (10  $\mu$ m) of cuticlelike appearance. Pedal pit tiny in contrast to large pedal gland. Pedal fold single to pallial cavity, sole glands numerous. Pallial cavity split into three superposed pouches: dorsalmost pouch surrounded anteriorly by vacuolated subepithelial gland cells (suprapallial glands) with dark-staining contents, posteriorly with two pairs of respiratory papillae; median pouch with secondary genital pore below anus; ventralmost pouch as short, single tube, flanked by a paired row of six pallial spines (Figures 3D, 7D). Copulatory stylets paired, large, accompanied by two pairs of shorter pallial spines, protruding into ventral pallial pouch. Dorsoterminal sense organ small, single, situated above terminal portion of pallial cavity, externally not visible.

Mantle epithelium with numerous glandular cells filled with deeply staining vesicles, no epidermal papillae protruding into cuticle. Transversal and longitudinal muscles of the body well developed, lateroventral longitudinal muscle tissue pronounced. Dorsioventral muscle bundles restricted to anterior body, forming three pairs of strong foregut retractors and constricting the dorsal midgut caecum.

Pharynx with thick layer of circular muscles, without epithelial gland cells. Radula (Figure 2C) supported by a complex composed of at least seven vacuolated bolsters, muscles and connective tissue, about 420  $\mu$ m long; radular sheath 80  $\mu$ m wide anteriorly. Paired anteroventral radular pockets short (in the present subadult specimens), containing the anteriormost five to seven radula bars of a total of 20 to 25 pairs. Radula bars almost rectangularly bent, 60  $\mu$ m broad, 9  $\mu$ m high (Figure 7C), with radular buttress in the region of the bend where bars are up to 12  $\mu$ m thick; with 17 pointed and moderately curved denticles which are longest (9  $\mu$ m) at buttress and one small denticle lateral to buttress. Ventral foregut glands as elongated ampullae embedded in muscle tissue of radular apparatus, composed of epithelial glandular cells containing either secretory vesicles or a deeply staining secretion. Esophagus short; midgut with anterodorsal caecum. Hindgut short, opening into dorsal pouch of pallial cavity.

Genital system of present specimens not fully developed: gonad small; gonopericardioduct paired throughout, pericardium spacious, tubelike ventricle on each end fixed to roof of pericardium; pericardioducts and seminal vesicles lacking; unpaired part of spawning duct surrounded by thick layers of circular muscles, paired ducts short, ending blindly. Epithelial cells of spawning duct large, pear-shaped, filled with dark-staining secretions. Single pair of copulatory stylets, evenly curved, slightly flattened terminally, 560  $\mu$ m long and 20  $\mu$ m in maximum width; copulatory stylet sheath with circular muscle layer and single protractor muscle consisting of very small fibers running from anterior part of sheath to posterior ventrolateral body wall.

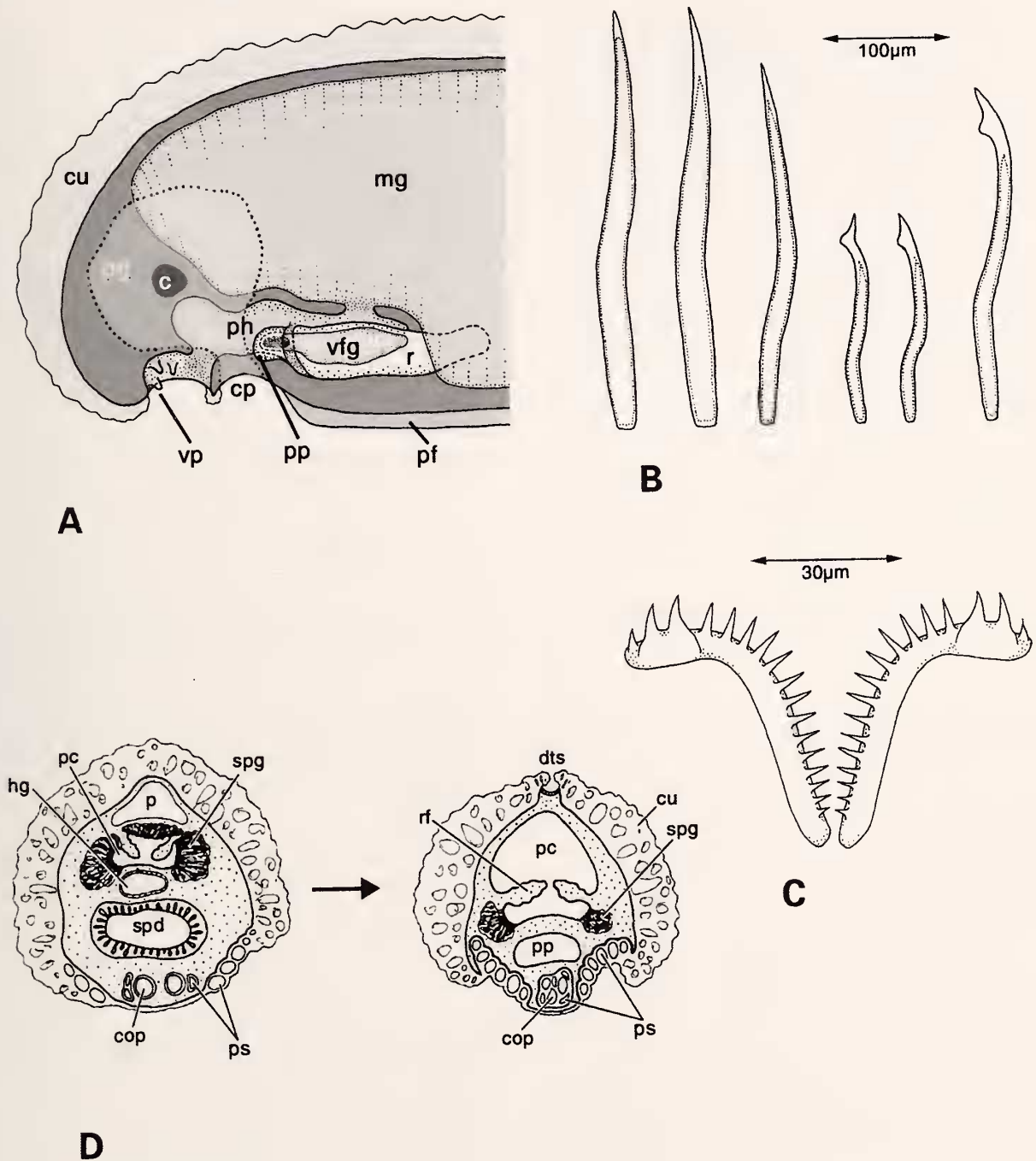


Figure 7. *Spiomenia praematura* Todt & Salvini-Plawen, sp. nov. A. Paratype 1, schematic diagram of the anterior body. B. Holotype, mantle spicules. C. Paratype 1, reconstructed pair of radula bars from the midregion of the radula. D. Holotype, schematic diagrams of cross-sections of the posterior body showing copulatory stylets and pallial spines, first cross-section anterior to second one. Key: c, cerebral ganglion; cop, copulatory stylet; cp, ciliary pedal pit; cu, cuticle; dts, dorsoterminal sense organ; hg, hindgut; mg, midgut; p, pericardium; pc, pallial cavity; pf, pedal fold; pg, pedal gland, indicated by dotted line; ph, pharynx; pp, pouch of pallial cavity; ps, pallial spine; r, radula; rf, respiratory fold; spd, spawning duct; spg, suprapallial glands; vfg, ventral foregut gland; vp, vestibular papillae.

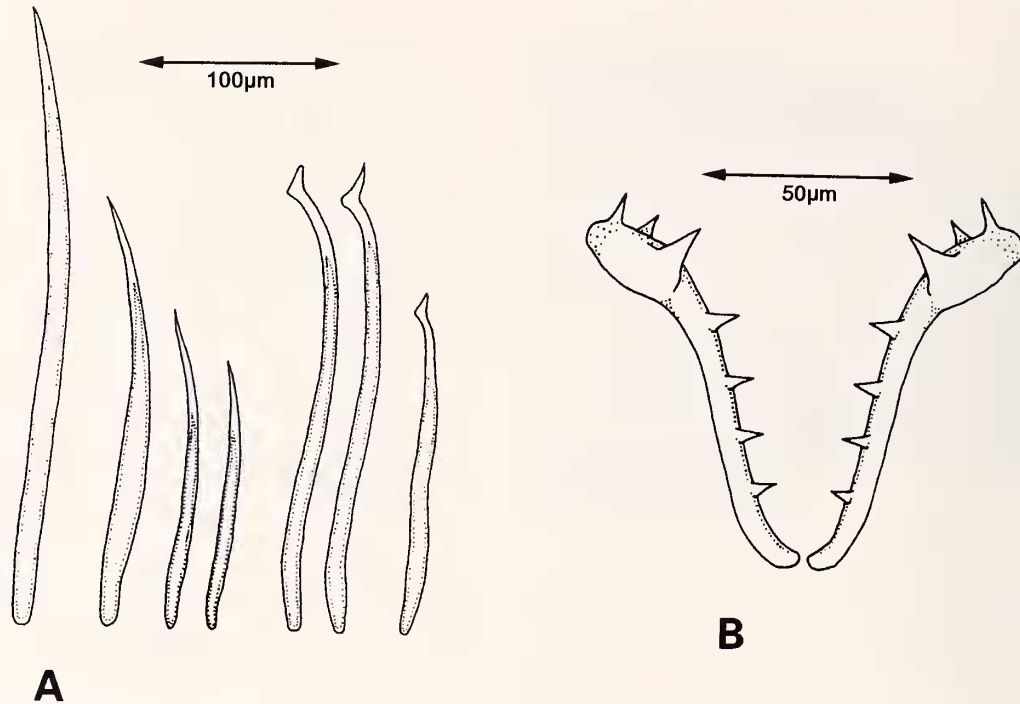


Figure 8. *Spiomenia phaseolosa* Todt & Salvini-Plawen, sp. nov. A, B. Holotype. A. Mantle spicules. B. Reconstructed pair of radula bars from the midregion of the radula.

**Remarks:** The immature state of the sampled specimens caused some uncertainties. The body length of adult specimens may reach more than 5 mm. Important features of the genital tract including seminal receptacles and/or vesicles are unknown. The ectodermal spawning ducts are present, whereas the mesodermal pericardioducts are not yet developed. The development of copulatory stylets apparently starts early in maturation, their dimensions in adult specimens are unknown.

Nevertheless, integument characters including the presence of the characteristic captate spicules as well as features of the radular apparatus and of the ventral foregut glands which are embedded into buccal muscle tissue justify a classification within the genus *Spiomenia*. In contrast to *S. spiculata*, *S. praematura* bears suprapallial glands but lacks a dorsal salivary gland. The denticles on radula bars of *S. praematura* are more uniform in size and there is only a single denticle lateral to the radular buttress, which is hardly pronounced and easily overlooked in histologic sections. A close relationship between the genera *Plawenia* and *Spiomenia* is indicated by the absence of skeletal spicules and of epidermal papillae as well as by radula morphology. The radula bars of species in both genera show an overall similarity with denticles laterally to the radular buttress occurring only in *Spiomenia*. The presence of captate mantle spicules in *Spiomenia* is the second character separating the two genera. However, whether this represents a true generic

(equivalent to other generic definitions in Solenogastres) or a subgeneric character remains open for forthcoming discussion when broader comparative information will be available.

**Etymology:** The species name *praematura* from Latin *prae* (before, early) and Latin *maturus* (mature) refers to the presence of copulatory stylets and pallial spines in an early state of maturity.

*Spiomenia phaseolosa* Todt & Salvini-Plawen, sp. nov.

**Holotype:** BENTHEDI (CENTOB) 87CH, 11°44'S, 47°35'E, 3716 m; mantle spicules (2 slides), series of histologic cross-sections (13 slides).

**Paratype:** Type locality; mantle spicules (1 slide), series of histologic cross-sections (4 slides).

**Diagnosis:** A small, spiculate species, mantle spicules slender, solid tips of captate spicules occupy 1/5–1/4 total spicule length; mantle without epidermal papillae; vestibulum with mostly branched papillae; radula bars thick, with seven denticles; gonopericardial system and pallial organs unknown.

**Description (Figures 1E, F, 2D, 8A, B):** Holotype immature, spiny, and stout, 1.7 mm long and 0.7 mm high. Mantle spicules slender, increasing in length from anterior



to posterior body region (Figure 1E). Vestibular opening triangular, pedal groove visible, pallial opening covered with spicules. Cuticle 40  $\mu\text{m}$  thick dorsally, 60  $\mu\text{m}$  ventrally. Mantle spicules (Figure 8A) thin-walled, of two types: acicular spicules, very slender, recurved, 70  $\mu\text{m}$  to 320  $\mu\text{m}$ , 4–10  $\mu\text{m}$  wide, with solid tips varying in length from 10 to 30% of whole spicule; captate (distally asymmetrically broadened) spicules 150  $\mu\text{m}$ –250  $\mu\text{m}$  long, 5–7  $\mu\text{m}$  wide, solid tip about 15–25% of total spicule length. Vestibulum spacious with numerous, partly branched papillae, up to 150  $\mu\text{m}$  long and 40  $\mu\text{m}$  wide. Pedal fold single, pedal gland large, sole glands regularly scattered along pedal groove, which ends anterior to pallial cavity opening. Dorsoterminal sense organ single.

Mantle epithelium with glandular cells, epidermal papillae lacking. Integumental muscle layers thin, longitudinal muscles ventrally pronounced; three paired dorso-ventral muscle bundles as buccal retractors, posteriormost pair constricting dorsal midgut caecum, resulting in a three-lobed formation of its anterior part.

Pharynx with thick circular and longitudinal muscle layers, dorsally lined by epithelial gland cells. Radula (Figure 2D) 240  $\mu\text{m}$  long with 20 pairs of plates; midregion of radular sheath 90  $\mu\text{m}$  wide, anteriorly wider with distance between paired radula bars growing, no true anteroventral radular pockets developed. Radula bars about 90  $\mu\text{m}$  broad, height ranging from 6  $\mu\text{m}$  medially to 12  $\mu\text{m}$  laterally (Figure 8B), thickness from 5  $\mu\text{m}$  medially to 14  $\mu\text{m}$  at lateral buttress. Dorsal margin of bars with seven denticles: denticles 1–4 evenly spread, innermost shortest, 2.5  $\mu\text{m}$  long, denticle 5 located on the radular buttress, 8  $\mu\text{m}$  long; denticle 6 about 6  $\mu\text{m}$  long and arranged at an angle to other denticles, lateralmost denticle in plane with denticles 1–4. Paired ventral foregut glands within muscle tissue lateroventral to radula, with narrow lumen, pores to pharynx laterally to radula. Esophagus short, midgut with anteroventral caecum, hindgut short.

Genital tract not yet developed with exception of posteriormost part of unpaired spawning duct. Ventricle fixed to pericardial roof over its total extension.

**Remarks:** The developmental status of the present specimens influences not only the gonopericardial tract but also the body shape (Figures 1E, F), as well as the formation of the anteroventral radular pockets. Nevertheless, epidermal spicules and radula plates demonstrate relationship to the genus *Spiomenia* as well as species-specific conditions.

**Etymology:** The species name *phaseolosa* from Latin *phaseolus* (bean) refers to the bean-shaped body outline.

## DISCUSSION

The species of Simrothiellidae sampled on the Benthedi cruise are classified in the genera *Simrothiella*, *Kruppomenia*, and *Spiomenia*. The low number of specimens,

however, leaves some questions open. These concern especially the anatomy of the gonopericardial tract in *Spiomenia praematura* and *Sp. phaseolosa*, where only immature animals were available. Scarcity of the material also precluded destructive methods to isolate radulae and copulatory stylets. Further sampling in the region would be desirable to fill in the gaps and to reconfirm details of internal anatomy and histology.

The Benthedi cruise revealed not only five new Simrothiellidae but also seven additional new Solenogastres species in five families (in preparation). Not a single species in the material could be identified as belonging to a published species. Taking into consideration that the Solenogastres fauna of the Indian Ocean has not been studied to date, the number of new species is not surprising. The fauna of the Indian Ocean north of 40°S including the Mozambique Channel is highly influenced by the Indo-Pacific region, whereas influence of the Antarctic Bottom Water flowing northward is not important in this region (Vinogradova, 1997). This may explain the lack of conformity to the Antarctic and Subantarctic Solenogastres fauna (Salvini-Plawen, 1978). Species descriptions from Indo-Pacific regions (Nierstrasz, 1902), however, are rare. Further research remains to be conducted to provide better insight into the species diversity of Solenogastres of the Indian and Pacific Oceans.

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